

TECHNICAL SERIES, No. 10.

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L. O. HOWARD, Entomologist.

THE SOCIAL ORGANIZATION AND BREEDING
HABITS OF THE COTTON-PROTECTING
KELEP OF GUATEMALA.

BY

O. F. COOK,

*Bionomist in Charge of Investigations in Agricultural Economy of
Tropical and Subtropical Plants.*



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LETTER OF TRANSMITTAL.

U. S. DEPARTMENT OF AGRICULTURE,
BUREAU OF ENTOMOLOGY,
Washington, D. C., April 22, 1905.

SIR: I have the honor to transmit herewith a paper on the social organization and breeding habits of the cotton-protecting kelep of Guatemala (*Ectatomma tuberculatum* Ol.), by Mr. O. F. Cook, Bionomist in Charge of Investigations in Agricultural Economy of Tropical and Subtropical Plants, Bureau of Plant Industry, and temporarily on duty in this Bureau for the purpose of continuing the investigations of this particular insect, whose cotton-protecting habits he was the first to describe. This report contains evidence to show that the breeding habits of the insect in question, especially its methods of founding new colonies, are essentially different from those of typical ants (family Formicidae) and resemble in important particulars those of the domestic honeybee. The possession of this type of social organization will, in Mr. Cook's judgment, greatly facilitate the establishment of the kelep in the cotton fields of the South if the insect should be able to withstand the change of climate and other natural conditions. I recommend that this paper be published as Technical Series No. 10. Another bulletin dealing more fully with the details of the life history of the species is being prepared and will be fully illustrated.

Respectfully,

L. O. HOWARD,
Entomologist and Chief of Bureau.

HON. JAMES WILSON,
Secretary of Agriculture.



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THE SOCIAL ORGANIZATION AND BREEDING HABITS OF THE COTTON-PROTECTING KELEP OF GUATEMALA.

INTRODUCTION.

In preceding reports treating of the kelep as an enemy of the cotton boll weevil the distinctness of its behavior from that of the true ants has been noted. To avoid in some measure the misapprehension likely to be caused by calling it an ant it seemed desirable to introduce with the insect its distinctive Indian name, *kelep*. In the minds of the natives of Guatemala, the kelep is not a kind of ant, but an independent animal not to be associated with ants. The more we learn about it the more this aboriginal opinion appears justified, not alone because the kelep is a beneficial insect, but because it has a different mode of existence and a different place in the economy of nature.

The popular classification of the social Hymenoptera recognizes three types—the ants, the bees, and the wasps, the ants being distinguished from the others by the absence of wings. The kelep falls, however, into none of these groups. To call it a wasp or a bee would not misrepresent the practical facts more than to call it an ant. In reality the kelep represents a fourth category of social Hymenoptera, as distinct from the other three as they are from each other. Authorities on the classification of the Hymenoptera have admitted a rather close affinity between the wasps and the ants, but the kelep differs from both of these groups and approaches the bees in important respects, and especially in those which affect the question of its domestication and utilization in agriculture.

It was naturally supposed at first that the kelep would have the same habits as the true ants which have been associated with it as members of the same family or subfamily, but the differences were greatly underestimated. If the Hymenoptera were classified by a taxonomic system consistent with that applied to the higher animals, the kelep would need to be recognized as the type of a new and distinct family. It is, moreover, the first member of its family of which the habits have become known. Under such circumstances it was quite impossible, obviously, to determine in advance whether its habits and instincts would permit its colonization in the United States and its use in agriculture.

The fundamental difference between the ants and the kelep, and that in which the latter resembles the honey bee, lies in the methods of swarming. Among the bees and the keleps swarming results

directly in the formation of new colonies, but the swarming of the ants is a distinct biological phenomenon having for its object cross-fertilization. The kelep is completely socialized, like the honeybee, while the ant is not. The keleps and the honeybees live only in communities, while the ants at one stage of their life history leave the nest and meet the vicissitudes of independent existence as solitary individuals, like the nonsocial insects. The social organization of the kelep represents a line of development distinct from that of the ants, and shows a relationship with the parasitic and predaceous wasps rather than with the true ants.

SWARMING AND OTHER TIME SPECIALIZATIONS.

The swarming of the ants is one of the many interesting phenomena which might be grouped under such an expression as biological synchronism. Species are organisms, or at least organizations, and in some of them there is manifested a simultaneity or time coördination of the numerous members corresponding to the orderly development of the cells of which the body of the individual is built. A flock of birds or a school of fish, with the individuals separated at equal distances and executing all their movements in exact unison, is a striking example of such synchronism, but other no less mysterious adjustments are necessary to enable animals and plants to keep so exactly the annual appointments by which the interbreeding of the members of the species is maintained. The climatic vicissitudes of temperate regions make complete simultaneity difficult, and have led us to ascribe the annual recurrence of events to the change of seasons rather than to recondite internal causes. The thirteen-year and seventeen-year trysts kept by the periodical cicadas over wide regions show, however, that more than sum totals of heat, cold, and food are involved, even in temperate climates.

Under the equable conditions of tropical existence, where the seasonal explanation entirely fails, there are biological events which might seem to show that plants and animals not only have drill-masters but time locks. Some of the Asiatic bamboos grow for thirty years or more by vegetative increase alone without producing flowers or fruit, and then all the members of the stock blossom, bear seeds, and die together, without reference to the age, place, or condition of the individual plants which may have been propagated from cuttings and carried to remote parts of the earth.

ANNUAL MATING CONCOURSES OF TERMITES AND TRUE ANTS.

Nests of West African "white ants," or termites, are crowded for weeks with winged individuals, but not one is to be found outside until some moist afternoon or evening, when the young sexual in-

sects emerge from all the nests of the species in the same hour. The air is filled as by snowflakes or a plague of locusts. Lights attract the flying insects, and are smothered under heaps of toasted termites. The insectivorous birds and reptiles gorge themselves to repletion. By the next morning the detached wings have been blown together in windrows, and nothing more is to be seen of that particular species for another year except by digging into their nests or galleries.

Probably not one pair of termites out of many thousands survive to become the parents of a new colony, but the purpose of the sacrifice is accomplished if these have secured the interbreeding necessary to maintain the incredible fecundity by which the termite queen furnishes the population of a community to be enumerated in millions. The mothers of such colonies have been seen to lay from 40 to 60 eggs per minute.

The true ants belong, of course, to an entirely different order of insects, and their social organization and swarming habits have been attained quite independently. Nevertheless some of them, and especially the families best known to entomologists, have a domestic economy and a morphological diversification of the members of the colony surprisingly paralleled to that of the termites, including the habit of annual mating concourses of sexual adults. There are in many species, both of ants and of termites, not only the two normal sexes and the sterile workers, but some of the last are further specialized in structure, instinct, and social duties as soldiers, foremen, nurses, etc. A family of American ants (*Cryptoceridæ*) also resembles a genus of African termites in maintaining an extensive and highly specialized system of fungus gardens.^a Other ants have domesticated plant lice, mealy bugs, and leaf hoppers for the sake of the honey dew secreted by these animals, which are herded,

^a With these fungus-cultivating ants and termites, at least, it would seem that a new colony can scarcely be founded by a pair of sexual termites or by a single fecundated female ant unless they carry their domesticated fungus with them. It is possible, however, that in both cases the newly mated insects are adopted and set up in housekeeping and farming by workers of their own species, who bring "spawn" of the fungi from the older colony with which they are in communication. This might the more readily happen because long subterranean galleries are a prominent feature of the architecture of the fungus-growing insects, both ants and termites.

The keleps, indeed, may be said to have taken a step toward the domestication of the cotton plant. They have at least adopted it, and show an instinctive interest and attraction for it in preference to other plants. That this also extends to a special animosity for the boll weevil as an enemy of the cotton is not, perhaps, to be claimed, but the habit of living on the cotton plant has resulted, no doubt, in giving the keleps a special familiarity with the boll weevils and a special skill in capturing and stinging them.

pastured, and cleaned with as much care as modern dairy cattle.^a Some ants have also a highly developed slave-making instinct, and undertake regular raids on the nests of other species to capture their young and carry them away to be brought up in servitude.

It would seem, therefore, that in the highest members of both groups of social insects the chief purpose served by this simultaneous emergence, or "swarming," as it is commonly called, is interbreeding, or cross-fertilization, rather than the founding of new colonies in more distant localities, as hitherto supposed. This may explain why the species of these insects have achieved nothing very remarkable in the way of geographical distribution, in spite of the immense fecundity of their females. A single individual ant or a pair of termites might be able to establish a *colony* in a new locality, but the lack of opportunities for cross-fertilization might prevent the perpetuation and further extension of the *species*, which could increase its range only by gradual, continuous expansion.

BREEDING HABITS OF THE KELEP.

With such instances in mind it becomes easier to appreciate the fact that the breeding habits of the kelep differ notably from those of the termites and termite-like ants, and approach those of the domestic honeybee. Although the actual migration has not been observed, there are strong indications that, instead of emitting annual broods of sexual individuals and founding colonies by means of solitary fecundated females, the kelep communities simply subdivide after the fashion of the bees, or in a still more practical and business-like manner, the problem of cross-fertilization having been solved in another

^a The extreme development of the pastoral instinct is to be found in an ant which takes care of the eggs of its plant-lice cattle through the winter.

"It is not merely that the ants milk them, defend them from attack, sometimes protect them by earthen inclosures from too great summer heat, but over and above all this they collect the eggs in autumn, keep them through the winter, and plant them out on their proper plant in the spring. Some of the root aphides may always be found in ants' nests, but I was much puzzled years ago by finding in ants' nests some black eggs which obviously were not those of ants. Eventually I ascertained that they belonged to a species of aphid, which lives on the leaves and leaf stalks of plants.

"These eggs are laid early in October on the food plant of the insect. They are of no direct use to the ants, yet they are not left where they are laid, exposed to the severity of the weather and to innumerable dangers, but are brought into their nests by the ants and tended by them with the utmost care through the long winter months until the following March, when the young ones are brought out and again placed on the young shoots of the daisy. This seems to be a most remarkable case of prudence. Our ants may not, perhaps, lay up food for the winter, but they do more, for they keep during six months the eggs which will enable them to procure food during the following summer, a case of prudence unexampled in the animal kingdom."—Avebury, 1905, *The Open Court*, 19:190.

way.^a The data which seem to support this conclusion are briefly summarized in the following paragraphs.

SIZE OF THE KELEP COLONIES.

The colonies, while very variable in size, range between 100 and 400 workers, and thus are of the same order of magnitude, instead of forming a series from solitary queens to communities of thousands or millions, as among the true ants and termites. Out of nearly 150 nests which have been explored only 3 or 4 had less than 100 workers. This fact alone was sufficient to place the kelep in strong contrast with the leaf-cutting ants, which are such conspicuous members of the insect fauna of Central America. The colonies of the leaf cutters contain enormous numbers of individuals, hundreds of thousands, or millions, perhaps; and yet the young queens begin alone. The small burrows of several such were found while kelep nests were being opened, the annual mating flight of the leaf cutters having taken place only a short time before.^b

Most of the colonies brought from Guatemala in the first importation were, as it now appears, mere fragments of normal communities, containing from 20 to 50 workers. The jars obtainable in Guatemala for use as cages were very small, and it was feared that overcrowding would be detrimental. It was supposed, too, on the analogy of the ants, that the colonies would readily replenish their numbers if conditions should prove favorable in Texas.

In the Texas experiments, however, it became apparent at once that in courage and general activity the behavior of the large colonies was very different from that of the small ones, a fact which the character of the social organization permits us to appreciate more fully than before. When permitted to do so the larger colonies generally moved with promptness out of the cages and established themselves

^a After the above was written Mr. McLachlan reported from Victoria, Tex., that there had been an increase in the number of colonies in two kelep settlements in the cotton field near that place. One wire-netting cage which had been supplied with four imported colonies was found to contain six colonies; another had seven colonies, though only five had been left in it. Before leaving Texas in October, I had noticed numerous young keleps in these cages, but had observed no addition to the original number of colonies.

^b It seems to be true, as the Indians say, that the leaf cutters are unable to establish themselves in territory occupied by the keleps. Presumably the keleps kill the leaf-cutter workers as soon as they come out of the ground, and the queen, being thus unable to raise a family to forage for her, soon starves to death. If there is a nest of leaf cutters near enough to a cotton field to make a raid upon it, the Indians protect it by a fence of tough leaves of the plant called *mosh* (*Calathæa*). The same leaves are used by the black "Caribs" of Livingston for lining the waterproof baskets which they weave from the climbing spiny palm (*Desmoncus*).

in new burrows of their own digging. Small colonies often refused to leave the cages. Large colonies took boll weevils as soon as offered, stung them, and carried them back into the nest to feed the young, while some of the less populous communities showed none of the hunting instinct and would tolerate the boll weevils for hours or even for days.

It has been observed, too, by many students of bees and other social insects, that colonies too much reduced in numbers may become listless and discouraged and fail to manifest their normal activities and instincts. To this rule the kelep is no exception; nevertheless, even in very small numbers or as solitary individuals they do not lose entirely their rational demeanor. This self-possession is probably a consequence of the habit of the keleps to spend considerable periods outside their nests patrolling the cotton plants, or standing motionless, waiting for boll weevils or other insect prey. The temperamental contrast with the honeybee in this respect is very striking.

The bee is above all, and even to a greater extent than the ant, a creature of the crowd. She can live only in the midst of a multitude * * * Isolate her, and, however abundant the food or favorable the temperature, she will expire in a few days, not of hunger or cold, but of loneliness. From the crowd, from the city, she derives an invisible alimient that is as necessary to her as honey.^a

POPULATION OF KELEP NEST THE SAME THROUGHOUT THE SEASON.

The numbers of the insects and young and other conditions inside the nests of the keleps in Guatemala have been found to be the same after an interval of over six months. The first exploration was made at the end of the dry season, in April, May, and June; the second at the end of the rainy season, in November and December. Numerous captive colonies also have been under continuous observation throughout the same period. No indication has been detected of any seasonal difference of habits, nor is it necessary to suppose that anything different takes place in order to explain the domestic economy and breeding habits of the species.^b

ONLY ONE TYPE OF WORKER.

The workers are all of the same form and of nearly the same size, with no indications of the existence of a first brood of very small individuals. In some colonies the workers average appreciably larger than in others, but there is no such diversity as among the true

^a Maeterlinck, M., 1901, *The Life of the Bee*, 30.

^b While this report has been awaiting publication the period of observation in Guatemala has been extended through the remainder of the winter and spring months. The maximum of breeding activity appears to fall in the dry season, at the end of the cotton-growing period, in March and April. Nests excavated by Mr. G. P. Goll contained in some instances over twice as many cocoons as adult insects. In other seasons this proportion is usually reversed.

ants. If colonies were established by solitary fecundated females, as among the true ants, some of the nests would have shown examples of the undersized workers, of which the first brood raised by the queen ant is regularly composed.

It is now a well-established fact that every ant colony is founded by a single fertilized female, or queen. The insect loses her wings and buries herself in a small cavity in the soil or wood that is to form the future nest. After entering the cavity she usually closes the opening so that she is completely shut off from the outside world. She deposits, at the expiration of a certain time, a number of eggs, and when these hatch as larvæ she does not go abroad in quest of food, but feeds her offspring with substances regurgitated from her own body. These substances are ultimately derived from the fat body, a store of nutriment accumulated during her life in the maternal nest, which she forsook to take the nuptial flight. Of course, the insect must derive her own nourishment from the same internal source, and as, in all ants, the development of the young extends over a considerable period of time, it follows that the larvæ are of necessity poorly fed, and after pupation hatched as dwarf workers (*microergates*). The number, too, of these diminutive creatures is limited, so that the whole colony in this incipient stage is a family consisting only of the huge mother and a few dwarf offspring.^a

Workers much smaller than any found in nature were raised in some of the captive colonies of keleps, doubtless as a result of unfavorable conditions or lack of the normal amount of animal food. Nests with diminutive workers would not furnish proof positive, therefore, that the kelep, any more than the honeybee, ever founds colonies by means of isolated queens. Disease, parasites, or starvation might be expected to bring about in nature, as in captivity, a condition which gives the kelep colony a superficial resemblance to a recently established community of true ants.

The finding of a colony of a few small workers of *Odontomachus clarus* has been reported by Professor Wheeler as evidence that the Poneridæ agree with other ants in the method of founding colonies. Other authorities on the classification of Hymenoptera recognize *Odontomachus* as constituting a family distinct from the Poneridæ by structural characters. Nevertheless, the similarity of habits between *Odontomachus* and *Pachycondyla* is so great that a difference in social organization seems very improbable. The fact that the *Odontomachus* nest found by Professor Wheeler was in a cavity in a stone may be the explanation of its unprosperous condition.^b

^a Wheeler, W. M., 1902, *Science*, n. s., vol. 15, p. 768.

^b Wheeler, W. M., *Science*, n. s., vol. 15, p. 769: "In a former paper I maintained that the Ponerinæ perhaps constitute an exception to the general method of establishing colonies, but I have recently found in a small cavity in a stone a fertile dealated queen of *Odontomachus clarus* surrounded by five diminutive workers. While it is certainly remarkable that one does not find similar incipient colonies of other Ponerinæ, this observation makes it probable nevertheless that the ants of this family agree with the Comptonotinæ, Myrmiciniæ, and Dolichoderinæ in their methods of founding colonies."

There is supposed to exist among the worker bees a division of labor, but nothing of the kind has been observed among the keleps, except that young individuals, which are easily distinguishable by their lighter color, remain in the nest for many days and perform nurse duty, while the foraging devolves upon the older and darker-colored insects.^a

The demoralization of some of our imported colonies may have been increased by the lack of a normal succession of young keleps to serve as nurses. The predaceous instincts of the older workers may incline them not only to neglect the larvæ, but to yield more readily to the cannibalistic tendency which some of the colonies have manifested.

KELEP COLONIES NOT HOSTILE.

Kelep nests are frequently placed only a few inches apart, the workers of the different colonies not being actively hostile. Members of two colonies will forage on the same cotton plant or tree trunk with no signs of animosity. Stranger ants introduced into captive colonies for observation have not been attacked. They usually receive little attention; if they enter the burrow they are likely to be brought out and carried to the boundary of the inclosure, but are released without injury. In nature such stragglers, if any, would merely be escorted to the border, as it were.

Under the social economy of the true ants the species consists of fewer and more scattered colonies of larger size. The workers from different nests often have as much animosity for each other as for members of distinct species. This hostility serves a practical purpose, the close proximity of nests being, among the ants, a distinct disadvantage. It is only in large and prosperous colonies that numerous sexual adults can be brought to maturity. Too many colonies close together would mean a general scarcity of food and would keep all the communities poor and unproductive.

The power of ants to distinguish at once between members of their own and of other colonies has long been recognized as one of the most remarkable refinements of instinct, and has been the subject of extensive study and experiment. A recent and extremely careful investigation has been made by Miss Adele M. Fielde, who finds that the

^a Some species of ants and of termites have a special caste of very small, slender workers which do not leave the nest, but are devoted to nurse duty. These might be looked upon as representing a social specialization by which the microergates are not confined to the first brood. On the other hand the very great specialization of the so-called soldier castes of the termites would seem to indicate that they are the oldest representatives of the worker series, and this view seems to be supported by the fact that the "workers" of *Calotermes*, which have the simplest social organization, are more like the soldiers of other genera than they are like the workers.

olfactory sense, through which the instinct of animosity to strangers is aroused, is so acute that ants will attack even their older sisters if they have been reared without contact with others of like age.^a

It is much better policy, from the standpoint of the social economy of the ants, for a given area to be occupied by one large colony than by many small ones, and with many of the ants this instinct of hostility is supplemented by that of retaining a part of the young females in the nest. This enables the community to be expanded to the greatest extent possible and avoids the waste of unnecessary competition and conflict.

The more amiable disposition of the keleps has enabled them to reach different and somewhat more democratic solutions of their social problems. They take better care of their young females, and do not find it necessary to make war upon their neighbors of the same species.

Like other carnivorous animals, the keleps become cannibals when driven by hunger, but in normal conditions of Indian agriculture an abundance of keleps in a locality would tend to increase the area planted to cotton, so that their existence would not be subject to the usual laws of competition in the struggle for existence.

Barring accidents which may compel a change of residence, an ant colony remains indefinitely in the same place, but the kelep organization is decidedly more mobile. Colonies can change their locations readily and may do so with promptness when a more desirable spot has been found. One of the ends gained by the kelep in moving would be to leave behind parasites, with which their nests sometimes become infested.^b

It is a familiar fact in the study of plants that some grow in clusters and others are solitary. If a seed produces only a single

^a Fielde, A. M., Biological Bulletin, 7:227. In some of the ants studied by Miss Fielde the aversion to strangers is said to extend even to a "manifest preference" of the females for males from the same colony. It should not be taken for granted, however, that the laying of eggs by queens captured before the mating concourse proves a previous mating inside the nest, nor that all the males which may be found in a nest originated in it.

^b The habit of frequent moving might also explain the apparent absence among the keleps of the guests or messmates which have attached themselves to many of the true ants. In Guatemala the kelep nests usually harbor a snail or two, a small diploped of the order Merocheta, a small creamy-white thysanuran, and a yormi which infests the bone yard or collection of dismembered skeletons of their prey, which are stored in a special underground chamber.

A few specimens of a hymenopterous parasite identified by Doctor Ashmead as *Isomaralia coronata* Westwood have emerged from some of the captive colonies during the journey to the United States, and even, in two instances, after they had arrived in Washington.

The worst enemy of the keleps, however, is a mite, which has become extremely numerous in some of the cages, especially those inhabited by small and demoralized colonies.

stalk the plants are solitary; if there are numerous buds and branches from roots or underground stems a cluster is formed and the plant is said to have a cespitose habit, depending upon the different method of reproduction. Similarly with the ants and the keleps the former have their colonies remote and hostile, the latter adjacent and friendly, or at least tolerant of each other. And though these differences might at first seem slight and insignificant, they result, in reality, from a fundamentally distinct system of social organization.

It is not only a regular and normal condition for ant colonies to be solitary and remote from each other, but there is a provision of mutual hostility which prevents the establishment of closely adjacent communities. The keleps, on the contrary, are social not only to the extent of forming colonies like the ants, but they are social to the second degree, as it were, in that the breeding habits of the insects provide for the normal existence of closely adjacent communities. Solitary kelep colonies would be as abnormal as closely adjacent ant colonies and as clearly at a disadvantage. Adjacent ant colonies might suffer for food, while a solitary kelep colony might meet extinction through inbreeding if the visits of males from other nests were excluded.

MALES CONTINUOUSLY PRESENT.

Winged males were found in the nests in about the same numbers in November as in June. They appear to be regular inhabitants and are received by all colonies with apparent indifference. They are agile, active insects and could readily pass from one colony to another, thus providing cross-fertilization without annual swarming. Males are not present in all the nests, and the number varied from 1 to 7 or 8, a diversity itself strongly indicative of the absence of the annual emergence, even of the males, at any stated time.^a The number of males had also no apparent relation to the number of females.

When the nests were opened in Guatemala the males often attempted to escape by running rapidly away, but did not take to wing, although Mr. Lewton informs me that some of those brought to Texas showed their ability to fly. They are, however, so active and fleet of foot that they could pass readily from one colony to another of the closely adjacent nests even without flying. Wingless males are known in some of the species of *Ponera*, and also in certain parasitic ants.

^a In Guatemala in the spring the number of males raised by some of the colonies was found to be much greater. Mr. Goll counted about 40 in one nest. Messrs. Kinsler and McLachlan saw numerous males at large in the cotton fields and observed, further, that they are often caught by the workers and carried down into the nests.

QUEENS INACTIVE.

The kelep queens, even when young, are distinctly less active than the workers. Isolated queens have shown no ability or inclination to excavate nests and very little interest in eggs or larvæ which have been intrusted to them.

It does not appear that the keleps have the art of regurgitating food for their larvæ or for each other, but they have, instead, the curious habit of opening their mandibles wide and lapping up drops of nectar, moistened sugar, or honey on their mouth parts. The liquid is thus carried into the nest and dispensed to the other members of the community, old and young. The queen is regularly fed in this way, though in a few instances the queens of captive colonies came to the surface to eat sugar with the workers.

In the true ants the young queen bites off her wings,^a excavates her own burrow, and cares for her first brood of eggs after having laid them, and appears not to be deficient in intelligence and activity in comparison with the workers. The demeanor of the kelep queens inside the nests differed notably from those of a species of *Formica* kept in the laboratory at Victoria, Tex., for purposes of comparison. The kelep queen is the last to notice any disturbance of conditions, such as the admission of light, but the *Formica* queens were even more nervous and irritable than their workers and were the first to run for shelter. The same was true of them when their nest was being dug out.

The only instances in which the kelep queens have shown any noteworthy activity have occurred when they were condemned to solitary confinement. As though realizing the uselessness of such an existence these queens often make reckless attempts at escape and run rapidly away, in complete contrast to their usual quiet and sluggish demeanor when associated with workers and eggs or young. In nature, or rather in the Guatemalan cotton fields, this activity on the part of a queen which had for any reason lost her family might be of advantage in enabling her to find a home with some other colony. Strange queens seem always to be welcomed when introduced into a new community with or without a queen of its own.^b The removal of the queen, on the other hand, does not seem to have any effect upon the actions of the workers as long as there are eggs and larvæ to care for, but workers alone become utterly listless and stand idly about with their

^a This was observed in Texas by Mr. Frederick L. Lewton in a young queen of *Cremastogaster laviuscula* Mayr.

^b In one colony studied by Mrs. Cook two strange queens, while not actually bitten, were dragged about in an unfriendly manner and did not long survive.

heads and antennæ in the air, as though waiting for something to happen.

There is no indication that under normal conditions the kelep queen ever leaves the nest voluntarily for mating purposes. There seems to be no record of a queen of this family being captured outside the nest. Mating inside the nest has been reported in another member of the family Poneridæ.^a Normally wingless females are also known in some of the other genera, which proves that with them, at least, the power of flight has been lost by the females as well as by the workers. In some species of ants and of Poneridæ there is no very sharp line between the workers and the queen, all of the intervening stages being occasionally found. Kelep queens and workers are, however, quite distinct, so far as observed. The queens are two or three times as large as the workers and are of a darker and more reddish color. The workers occasionally lay eggs, but they are of a distinctly smaller size than those of the queen. They remain white instead of turning a deep gray or blackish, like those of the queen, and are apparently recognized as worthless, for they are at once fed to the larvæ, a fact discovered by Mr. F. L. Lewton.^b

When there are no larvæ the keleps seem not to know what to do with these diminutive eggs, but continue to carry them around in their mandibles. In one small colony I have seen three worker keleps with eggs at the same time, which would seem to indicate either that they are laid in considerable numbers or that they are carried about for considerable periods.

The wings of the female being useless, it might be expected that they would be bitten off as promptly as in the true ants, or even sooner, but this is not the case. It seems scarcely possible that the queen could bite them off herself, even if so inclined, and of such an instinct there is no indication. The wings seem to be worn for an indefinite period. Queens with one or both wings frayed to half their length or less are occasionally found. The wing stumps, also, are of irregular sizes. It seems not unlikely that the workers gnaw them away gradually as a part of the cleaning process.

In *Pachycondyla*, as described by Professor Wheeler, and in *Neoponera*,^c which occurs in the vicinity of Victoria, Tex., the queens

^a Wheeler, W. M., 1901, Biological Bulletin, 2:49.

^b The laying by workers of eggs of nearly normal size which also turn dark and seem likely to develop normally was reported from Victoria, Tex., by Mr. Argyle McLachlan, after the above was written.

^c The species of *Neoponera*, which commonly lives in the mesquite bushes about Victoria, has been identified by Doctor Ashmead as *N. villosa* Fab. It is not without interest with reference to the possibility of establishing the kelep in Texas that the distribution of *Neoponera villosa* extends from Texas to Brazil.

and workers are very nearly of the same size, and, except for the possession of wings by the former, look quite alike, while in other genera, like *Leptogenys*, the females, though wingless, are very different from the workers. Such facts might have served as indications of considerable latitude of social specialization in the family as a whole, as abundantly shown when the kelep is added to the series.

The Poneridæ with wingless females seem to ally the group still further with the Dorylidæ and Mutillidæ and increase the contrast with the true ants, where the wings still remain as essential for the females as for the males. It may be needless, perhaps, to add that it is the loss of the wings by the workers and by the queens which marks the course of recent evolution in the Hymenoptera as a whole, as in all other insects. The most primitive insects were winged; all the wingless insects are descended from winged ancestors.^a The fact that so small a proportion of the members of an ant colony have wings, and these for so short a time, tends to make it appear that the wings are a special provision, while in reality the specialization is all in the direction of winglessness. The ants are in this respect more primitive, since they have preserved a character which is being lost in the Poneridæ and which has entirely disappeared in the Dorylidæ, Mutillidæ, and Thynnidæ.^b

The winglessness of the queens has been attained, however, by an evolutionary step distinct from that which resulted in wingless workers, and has a very different significance from the standpoint of the social organization of the species.

The winglessness of the workers may be looked upon as a part of the general stunting and sterility of the individual for lack of adequate food. In the early stages of the development of a new colony it is undoubtedly an advantage not to have too many larvæ, which would increase the danger of starvation for the whole lot.^c The loss or disuse of wings by the sexual females of parasitic wasps, drivers, and Poneridæ, on the other hand, is a sequel of the abandonment by

^a Cook, O. F., 1902, The Earwig's Forceps and the Phylogeny of Insects; Proc. Entom. Soc. Wash., 5: 84.

^b Winglessness of one of the sexes also occurs in several anomalous ants which live as parasites in the nests of other species and establish no independent colonies of their own. In the genus *Tomognathus* the male is winged, but the female is wingless and workerlike. Insects from the same nest have been found not to pair. In the genera *Anergates*, *Formicorenus*, *Symmyemica*, and *Cardiocondyla* the conditions are reversed, the males being wingless and similar to the workers, while the females have normal wings.

^c The storing of honey by the bees had for its primary purposes, we may believe, the avoidance of temporary stringency of food during the period of brood rearing, not the laying up of supplies to enable the adult members of the colony to pass the winter. The storing habit enables the bees to occupy temperate regions, but tropical bees also accumulate supplies of honey.

that sex of the habit of flight, which means that the social organization of the species is essentially different from that of the true ants, in which both sexes emerge into the open air for a marriage flight.

MIGRATION OF COLONIES.

In the transfer of a colony of keleps from one nest to another the workers take the initiative. After an excavation has been made eggs and larvæ are carried over. First attention is given to the eggs, the possession of which renders the new colony in a measure independent of the presence of a queen. Even before the new burrow is dug some of the workers load themselves with eggs and stand ready to carry them in.

The ancient popular theory that the communities of the social insects are organized on a monarchical basis finds little support in the way of detailed facts. It has long been known that the nervous system of worker bees and ants is more highly developed than that of the sexual insects, and especially the parts which correspond to the brain of higher animals. Even in the most highly organized society of the termites the workers are the intelligent and efficient part of the community, the queen having no other function than the laying of the eggs from which the huge family is hatched. The termite "mother," as the Africans more correctly call her, becomes enormously distended and completely unable to move. She is kept with her mate in a special chamber with very small entrances through which only the workers can pass, and even these openings are promptly sealed up with earth when the colony is attacked. Among the nomadic "driver ants" the mother of the colony does not lead the procession and never goes abroad in daylight. The natives of Liberia say, however, that in rare instances she is seen at night being hurried along by her numerous family.

Among the honeybees, also, the workers, rather than the queen, take the initiative in matters of the internal management of the colony which lead up to swarming. Unlike the keleps, the bees do not carry eggs or larvæ with them, and are hence completely dependent upon the presence of the queen to insure the perpetuation of the new colony.

QUEENS CARRIED BY WORKERS.

If the kelep queen does not follow at once to the new nest a worker seizes her by the mandibles, raises her in the air, and carries her over bodily. This has been observed repeatedly in connection with the prompt transfers which many of the imported colonies made from their cages into the ground. The queen submits to this treatment as though it were a regular occurrence, and remains quiet and rigid while being carried about. In one instance several workers also re-

mained behind, but were caught and carried by their sisters into the new burrow. This simple expedient avoids many difficulties and complications. The queen need not be possessed of any instinct of leading or accompanying the swarm, as among the bees, and there is no danger of her becoming lost as a result of her comparatively deficient instincts.

The large straight-edged mandibles of the kelep are well adapted for holding or carrying objects of considerable size. Ants with smaller jaws could not catch and sting boll weevils, because they could not hold them in the right position. Numerous ants may be said to *attack* boll weevils, but are able only to seize them by the legs or snouts and drag them about for a time. As soon as released the weevil escapes by its well-learned trick of feigning death. The kelep can pick the weevil up bodily, and in normal positions on the stems of cotton plants can usually sting it while the weevil is still "playing possum," before it begins to struggle. It is accordingly not without interest that the large mandibles and long legs which qualify the kelep as a weevil destroyer have other important functions in the social economy of the species.

It may be mentioned also, as showing the special efficiency of the keleps in moving their domicile, that they seldom carry one egg alone, but will often go to considerable pains to pick up two or three at a time. Sometimes the eggs adhere in considerable numbers, though not as in *Odontomachus*, where they are cylindrical and are made up into compact bundles. Eggs, pupæ, and other objects are frequently pushed between the mandibles by the end of the abdomen, brought up from below as in stinging the boll weevil. Two cocoons are sometimes packed up in this way, so that they can be carried together. It is also by virtue of this same flexibility of the abdomen that the workers are able to assist themselves with their mandibles in the laying of the undersized eggs which they occasionally produce.

DIVISION OF A COLONY.

A colony with two queens spontaneously divided into two by the departure of some of the workers and one of the queens. This incident was observed in Victoria, Tex., by Mr. Frederick L. Lewton, the essential facts being stated as follows:

On July 22 the ants in colony No. 26 exhibited signs of restlessness, and as several had been found dead a new nest was prepared in a larger jar. The two jars were connected by means of a cotton-leaf bridge. The dead ants were immediately carried over to the new jar and also the hard remains of several boll weevils. A considerable amount of earth was also carried from the old nest to the new, but few ants remained in the new jar until its lower half was protected from the light. The protection was removed from the old jar, which was also allowed to become dry, in order to hurry the keleps in removing the colony.

At the beginning of the experiment a number of eggs and larvæ were on the surface of the soil in the old nest. One larva was almost fully grown and about ready to pupate. In twenty-four hours all the eggs and larvæ, except the large one, had been removed to the bottom of the new jar, while the one remaining in the old nest had been taken below and covered with loose earth preparatory to pupating.

In another twenty-four hours there seemed to be almost no communication between the two jars and a close inspection was made. Then it was found that the old colony had contained two queens. One of these had taken possession of the new nest, accompanied by about half the workers and all of the eggs and young larvæ, only the full-grown larva and the workers remaining with the other queen in the old nest. This she would not desert, in spite of the strong light and the dryness. The jar was therefore moistened and protected from the light, and within five days the queen began laying again. The one larva began spinning its cocoon on July 23, and it was finished in about three hours.

COLONIES FOUND WITHOUT QUEENS.

Several kelep colonies containing eggs and larvæ were very carefully explored in Guatemala without finding queens. In view of the simple structure of the nests and the extremely favorable circumstances under which the work was done, it is not considered probable that the queens escaped notice in all these instances. It seems more likely that some of these colonies had been established recently without queens.

REPLACING A QUEEN.

Captive workers alone, as already stated, become listless and confused, but if supplied with eggs their behavior soon becomes normal. Several queen larvæ have been raised in the laboratory at Victoria, Tex., the first two in a colony in the hands of Mr. W. E. Hinds, the others by Mr. Argyle McLachlan. One might argue from Mr. Hinds's experiment great intelligence on the part of the keleps. One of two colonies had lost its queen by an accident, but was supplied with eggs from another on the supposition that a queen would be raised to make good the deficiency. The keleps appeared, however, to have no special desire to have a queen to support as long as they could secure a regular supply of eggs, and continued to raise workers only. The other colony, however, from which the eggs were being removed, took measures at once to raise a new queen, the deficiency of eggs having given, perhaps, the impression that the fecundity of their queen was declining. Two larvæ of unusual size were raised, one of which emerged as a normal winged queen. Mr. Hinds found that the time required for the development of a queen is about three months, the larval and pupal stages being about one and one-half times as long as those of the workers.

Two queens raised by Mr. McLachlan in January and February,

1905, spent $35\frac{1}{2}$ days in their cocoons, a period distinctly less than that of two worker pupæ of the same colony at the same time, which took $40\frac{1}{2}$ and 39 days, respectively. These queens were raised in the same queenless colony previously referred to, after the supply of fresh eggs was cut off. This would seem to show that a scarcity of eggs rather than the bodily absence of the queen may be necessary to set the workers to the development of a new queen. Certain it is that there is no such obvious reaction to the presence of a queen as among the bees. If the accounts of Maeterlinck and other observers are to be credited, there would seem to be among bees either a distinct system of royal etiquette or some direct unexplained influence upon the actions of the workers.

And one may mention here the curious fact that the workers always avoid turning their backs on the queen. No sooner has she approached a group than they will invariably arrange themselves so as to face her with eyes and antennæ, and to walk backwards before her. It is a token of respect, or of solicitude that, unlikely as it may seem, is nevertheless constant and general.^a

TYPES OF SOCIAL ORGANIZATION AMONG INSECTS.

Insects of several natural groups might be described as social. The larvæ of certain Lepidoptera remain together and even make community webs or cocoons. Some of the bark lice (Psocidæ) also pasture in droves, and in their younger stages spin continuous silk canopies over their feeding places. These communities, while obviously held together by social instincts, are in no proper sense to be termed organized, no division of labor or diversity of form or structure having arisen as a result of the merely gregarious association of individuals. Among the Hymenoptera some of the wasps of the family Eumenidæ represent this primitive social condition. Maeterlinck has traced the social development of the honeybee.^b

For an adequate outline of the diversity of breeding habits it seems necessary to recognize at least six types of social organization among insects. The contrasts between the different biological conditions found in the several forms of insect society can best be shown by brief formal descriptions.

^a Maeterlinck, M., 1901, *The Life of the Bee*, p. 214.

^b "We find even to-day, among the melliferous Hymenoptera, all the stages of progressive civilization of our own domestic bee. At the bottom of the scale we find her working alone, in wretchedness, often not seeing her offspring (the *Prosopis*, the *Colletes*, etc.); sometimes living in the midst of the limited family that she produces annually (as in the case of the humblebee). Then she forms temporary associations (the *Panurgi*, the *Dasypodæ*, the *Halicti*, etc.), and at last we arrive, through successive stages, at the almost perfect but pitiless society of our hives, where the individual is entirely merged in the republic * * *."—Maeterlinck, M., 1901, *The Life of the Bee*, p. 31.

THE TERMITE SOCIETY.

Interbreeding maintained by a simultaneous annual concourse of all the recently matured insects of both sexes.

Colony founded by a pair of sexual insects which remain permanently mated.

Wings provided with transverse sutures which enable the insects to break them off readily by an upward bending of the abdomen. Both sexes shed their wings in this manner as soon as they have associated in pairs, and then begin digging in the ground.

Workers of both sexes always wingless, numbered by thousands or even by millions, generally of diverse form, or of two or more distinct castes—soldiers, nurses, etc.

Several of these features are not shared by any of the types of organization found among the bees, wasps, ants, or other Hymenoptera. It is only among the termites that the males are regularly found with the females in the nests. Among the Hymenoptera the males are relatively short-lived and take no part in the work of the colony. Sometimes they are not even tolerated in the nests. A single fecundation suffices for the lifetime of the queen bee or ant, while among the termites the process is probably repeated. Copulation has never been observed among the termites; it does not take place during the mating flight, as among the bees. The wings of Hymenoptera are not provided with sutures to render them easily detachable. Males are permanently winged in all the groups; in some the workers are wingless, and in some the females also. Among the ants the queen is artificially wingless, as in the termites. She bites off her own wings after the marriage flight.

Perhaps the most fundamental peculiarity of the termite organization lies in the fact that the workers, soldiers, nurses, or whatever the various castes may be called, are of both sexes, instead of being undeveloped females only, as among the bees and ants. Whether a young bee larva shall develop into a queen or become stunted into a worker or so-called "neuter" depends upon the quantity, and perhaps also the quality, of the food supplied to it. Among the honeybees special brood cells are prepared in advance for the males, the workers, and the queens which the colony proposes to raise.

EXPLANATIONS OF WORKER CASTE.

It has been supposed that the differentiation of the members of termite colonies is governed in the same manner, by nutrition merely, but this is rendered very doubtful by the fact stated above, that the workers of all the different castes represent stunted individuals of both sexes. Another serious weakness in the nutrition theory lies in the fact that the larvæ of the termites are not mere helpless, inactive grubs, as in all the social Hymenoptera, but are quite as capable of locomotion as the adult workers, and are always traveling about to

all parts of the nests, so that the application of a consistent regimen of feeding would become, humanly speaking, impossible.

In some of the relatives of the kelep native in Texas, Professor Wheeler has found that there is no clear distinction between the fertile females and the workers, a condition which he ascribed to the desultory feeding habits of the insects.^a The deficiency may be connected, however, with the more backward social organization of the Texan species. The keleps, with the same predaceous habits, seem always to be able to produce the two well-defined types; at least no intermediate forms have been observed.

The question has not been put to an experimental test as yet, but the suggestion has arisen in connection with the kelep that the development of a larva into a worker may be brought about in the early stages by withholding food, it having been noticed that the larvæ grow very slowly at first, but after they reach a certain size they often complete their development with great rapidity. A superabundance of food or a special solicitude for the younger larvæ might induce the development of queens without the necessity of supposing that the insects proceed by any deliberate intention.

But even among the keleps the worker caste is hardly to be explained merely by inadequate nutrition, for the reason that it possesses positive as well as negative characters and instincts which the queens do not have, and which they probably never had in the evolutionary history of the species. As previously stated, it is well known that among the bees and ants the nervous system, and especially the part which corresponds to the brain of the higher animals, is much more highly developed in the workers than in the sexually perfect insects, and this is accompanied by the accentuation in the workers of the social instincts by which the colony is maintained.

HIGHLY SPECIALIZED WORKER CASTES.

The more recent evolutionary changes among social insects have been largely in the direction of the workers, the males and females

^a "Now, while we can, perhaps, understand how these more specialized ants may manage to control the quantity and quality of liquid food regurgitated from their own crops and salivary glands, it is not so easy to understand how ants can exercise such control when they adopt a capricious method of feeding like that of the Ponerinæ. Such a method can hardly produce clear-cut results, i. e., either workers or fertile females. And a comparative study of the better-known species of Ponerinæ shows that in certain species, at least, there is no such sharp distinction between the sterile and fertile female as we find in the more specialized ants. Not only is the female sex in a state of morphological and physiological instability—i. e., di- or even tri-morphic—but the male sex also is sometimes dimorphic, at least in the same genus, if not in the same species."—Wheeler, W. M., 1901, *Biological Bulletin*, 2: 28.

retaining more nearly the characters and habits of their nonsocial ancestors. The development of the workers has not been confined, however, merely to the more highly specialized nervous system and instincts. In many of the ants and termites there are two, and sometimes three or four, distinct kinds of workers, very different from each other and equipped with an equal diversity of instincts for undertaking special parts of the work of the social organization. One of the African termites has soldiers with immensely large heads and biting mandibles, whose sole function is that of defending the colony. When the wall of the nest is broken they sally out to engage the intruder. They are wholly devoted to this purpose, and lack even the instinct to return again, and soon perish from exposure to the drier, outside atmosphere. A second form of worker, also with large heads, but much smaller jaws, will not leave the nest to fight, but appears to control the erection of new walls, though it does not itself carry earth, a work performed entirely by the third caste, which might be called the worker proper. These build the nests and bring in the dead wood, which, after a period of curing, is made into fungus gardens. The fourth caste is small and slender, and neither fights nor carries earth, but is occupied with the management of the eggs and, presumably, also with the feeding of the young larvæ.

We may be sure that this high degree of specialization of castes has come about during the period of social organization. How the queens are able to give birth to these distinct kinds of offspring is unexplained as yet, either by difference of nutrition or by any of the theories of hereditary transmission applied to the other groups of animals.

Professor Weismann has appreciated the inadequacy of the nutrition theory, even with reference to the honeybee, and has attempted to explain the worker caste by means of his well-known theory of determinants.^a

^a " This explanation [nutrition], however, even if correct as regards the degenerated parts of the workers, does not sufficiently account for the other differences between the two kinds of females. For the workers are not inferior to the queen bee in all respects. On the contrary, the worker's sting is straighter, longer, and stronger, and is provided with more teeth than the queen's. The wings, moreover, are longer, the tarsal segment of the hind limb is provided with the well-known brush, and the tibia has a depression known as the 'pocket' for carrying the masses of pollen which the insect collects. These two characteristic parts are wanting in the queen. Important differences must also exist as regards the minute structure of the brain, for the instincts of the queen are very different from those of the workers. After fertilization has taken place the queen lays eggs, but she neither gathers honey from flowers, excretes wax, nor makes the honeycomb. It is therefore incredible that the queen and workers should be formed by the agency of similar determinants.

It is apparent, however, from what has been said regarding the termites of Liberia that Professor Weismann has greatly underestimated the difficulties which his theory of heredity would encounter in that group. As the various castes are not separated on sexual lines, there are five forms of each sex, or possibly six if complementary or substitution royalties are developed. Instead, therefore, of three or four kinds of determinants there would need to be ten or twelve kinds, and since it would be necessary to provide in the same way for the preliminary stages of the various castes more than a score of different determinants would need to be predicated—too many, it would seem, to leave us much confidence in this method of accounting for the existence of the worker caste.

THE ANT SOCIETY.

Interbreeding maintained by a simultaneous annual concourse or mating flight of all the recently matured insects of both sexes.
Colony founded by a solitary fecundated female.
Wings present on young females, but bitten off after the mating flight.
Workers always wingless, often to be numbered by thousands, commonly of diverse form or of two or more distinct castes. Workers of different colonies of the same species actively hostile.

Numerous deviations from this type of organization are to be expected among the various families of the tropical ants, the habits of which are still very imperfectly known. The colonies of many ants, too, are compound, a part of the young females remaining in the parental nest. Miss Fielde describes such a colony of *Stenamma*

The germ plasma must contain double determinants for certain parts of the body of the queen and workers, respectively. But as we have already assumed the existence of double determinants for the formation of male and female bees, or at any rate for the development of those parts which differ in the two sexes, we can only make the further assumption that the 'female' halves of the double determinants may themselves consist of two halves, corresponding to the queen and worker, respectively, and that each of these halves must naturally be looked upon as a complete determinant as regards size and structure. * * *

In the case of bees the factor that determines which of the two halves of the 'female' determinant is to become active seems to be the quality of the food supplied to the larva, so that the critical moment only arrives long after the termination of embryogeny and before the chrysalis stage is reached. * * *

We might, however, also assume the existence of three independent determinants side by side, so arranged that they become active under other definite influences, and this conception would better agree with the unavoidable assumption that the three determinants which act vicariously are of a similar size. * * *

The termites, in addition to the workers or stunted females, possess "soldiers," or males in which the sexual organs are stunted, which possess very strong mandibles and differ in other important structural details from the ordinary males. In this case, therefore, four determinants must be present, each capable of being substituted for another, and only one of which can be active at a time."—Weismann, A., 1893, *The Germ Plasma: A Theory of Heredity*, 377-379.

fulvum scattered over an area 90 yards in diameter, and states that she has been "unable to find any other colony of *Stenannas* in its vicinage."^a

THE BUMBLEBEE SOCIETY.

Interbreeding maintained by free flight of males during the period of emergence of young females.

Colony founded by a solitary fecundated female, the males and workers not surviving the winter.

Workers permanently winged like the sexual adults.

The organization of many of the social wasps is essentially the same as that of the bumblebee. This close similarity of social habits has been accepted by many entomologists as an evidence of relationship between the two groups, but the present tendency is toward the view that the social organization has been attained independently.

THE HONEYBEE SOCIETY.

Interbreeding maintained by the free flight of males during the swarming season, when they are permitted to feed in any of the nests. The young queens emerge from the nests for a nuptial flight, in which fecundation is accomplished.

Colony established by subdivision of the workers of an older swarm, accompanied either by the old queen or by a young queen still unfertilized.

Males short lived, usually not tolerated in the nests except during the period of emergence of newly adult females.

Females permanently winged, but the wings used, normally, only in the nuptial flight and in that of swarming.

Workers permanently winged, of one caste, or of slightly different castes, numbered by thousands. The workers of different colonies are not actively hostile except to marauding intruders.

THE KELEP SOCIETY.

Interbreeding probably maintained by the visits of the males to the various adjacent nests; no concourse or nuptial flight of females.

Colony established by a body of workers from an older community. The workers carry eggs, larvæ, and queen with them for the complete equipment of the new nest.

Males permanently winged, but apparently not inclined to fly; tolerated in all nests, and probably present throughout the year.

Females winged at first, but not known to fly or emerge from the nest.

Workers wingless, all of one form or caste, numbered by hundreds; not actively hostile.

In other genera of the same family normally wingless queens are frequently found. In some only wingless queens are known; in others some are winged and others wingless, with no differences in other

^a Fielde, A. M., 1904, Biological Bulletin, 7: 245.

respects. Fecundation inside the nest has also been observed in a member of the Poneridæ, or kelep family, as already noted.

Though no doubt attained independently, the resemblance of the kelep social organization to that of the bees is fully as striking as the parallel between the ants and the termites. The most serious difference lies in the fact that the queen bee must go out of the nest to be fertilized. Both the keleps and the bees are able to raise new queens as long as eggs are obtainable, but the danger of failure is much greater with the bees because of the vicissitudes of the marriage flight to which the young queen is subjected. In the habit of an open-air mating the bees resemble the butterflies, dragon flies, and other nonsocial insects. Mating inside the nests represents a more advanced and much more practical social system.

It is not difficult to assign a reason for a frequent subdivision of colonies as a feature of the social economy of the kelep. A large colony of predaceous insects would soon exhaust the insect fauna of its immediate neighborhood. It could maintain itself only as the drivers do, by foraging widely and changing quarters frequently. The keleps do not go, apparently, more than a few feet from their burrows. They seem ready to move their nests to more favorable locations, but these migrations are also, in all probability, for short distances only, though the Guatemalan Indians say that the keleps will come in from neighboring areas and occupy a cotton field after the crop has been planted.

THE DRIVER SOCIETY.

Interbreeding maintained by annual emergence and free flight of large numbers of males.

Colonies nomadic, probably increasing by the subdivision of migratory hordes.

Larvæ carried about by the workers for long distances.

Females wingless, probably never emerging from the nest unless carried by the workers.

Workers wingless, of two or more castes—soldiers, nurses, etc. Numbered by hundreds of thousands, or millions.

The African "drivers" and the army ants of the American tropics represent another group of social insects popularly associated with the true ants because the workers are wingless. In Liberia the males sometimes fly to lights in the evening in large numbers, which may indicate a definite breeding season for the sexual adults. Most Dorylidæ have been described from workers and males, very few females being known to science. The winglessness of the females may be said to advertise the distinctness of their social economy from that of the true ants, and to ally them with the Mutillidæ. Doctor Ashmead has

also pointed out to me the strong similarity of the males of *Dorylus* to those of the wasps of the East Indian *Vespa doryloides* Saussure.^a

The scant evidence thus far obtained seems to show that a colony of drivers has only one large, distended queen, like that of the Termites. Emery notes that the last joints of the legs are usually broken off in the specimens known to him.^b Such mutilation may well arise while the huge creature is being dragged about, as stated by the native Africans.

The interesting feature of the drivers, from the standpoint of the study of the kelep, lies in the fact that the differences between them and the true ants are in several respects the same, though much more accentuated than between the ants and the kelep. Thus, interbreeding is accomplished in both groups by the circulation of the males, the females, apparently, never emerging from the nests. The drivers carry their larvæ, and presumably their queens also, for long distances, their close ranked, rapidly moving columns sometimes requiring several hours to pass a given point. In food habits, too, they are carnivorous, like the keleps. They not only capture insects and other arthropods, but young or helpless vertebrates also. Active creatures even, like rats and mice, are often secured, the pain inflicted by the bites of the drivers causing them to roll about on the ground and thus permit more and more of their diminutive enemies to attack them. Any animal too large to be carried away by a single worker is cut in pieces. The kelep follows the more social plan of moving large insects and centipedes by the combined strength of several workers. The drivers are also like keleps in having a sting which they do not use as a weapon of offense against man, but they bite viciously and will not let go, even though their bodies be pulled loose from their heads.

The association of the keleps with the drivers permits a better appreciation of their habits in two respects. First, the apparently high development of their instinct of place or ability to find their way about, even in new situations. The drivers are fierce warriors,

^a Doctor Ashmead informs me that the males of the tribe Amblyponinæ, near relatives of the kelep, are very closely similar to those of the Mutillidæ, even to the structure of the petiole and the venation of the anterior wings.

The flying to lights of the males of the Dorylidæ, or drivers, is also shared by the males of *Myrmosa* and related genera of parasitic wasps formerly placed in the Mutillidæ, but which Doctor Ashmead now separates as a distinct family, Myrmosidæ, intermediate between the Mutillidæ and Vespidæ, but having wingless females like the Mutillidæ and the Dorylidæ. Some of the Bethyloidæ also have wingless females, but these are not supposed to have any close affinities with the other families. The Thynnidæ, which have been thought to connect with the Mutillidæ and the ants, likewise have wingless females. Finally, a few of the Mutillidæ are wingless in both sexes.

^b Emery, E., 1895, Ann. Soc. Entom., France, 64:73.

which actively pursue and capture their prey. They are to be described as predatory, while the keleps are merely predaceous, and like many other predaceous animals their movements are slow and deliberate except when they make a final spring to seize their game. The slow movements of the kelep thus conduce to its efficiency as a hunting insect, and may be looked upon as an evidence of specialization in this direction. *Odontomachus* and the Texan *Poneridæ*, so far as observed, are quicker and more excitable under ordinary circumstances, but they seem not to have developed any such skill in capturing quick-moving insects. The similarity of the keleps to the drivers is greater, however, when the colony moves and the eggs, larvæ, pupæ, cocoons, and queens are carried over to the new burrow. In one instance a few of the workers refused to leave the old nest, but the majority would not permit the colony to be divided in this way and finally captured and carried off the unwilling members in the same way that the queen is removed. One of the Brazilian relatives of the kelep is described by Bates as marching about in the forests in a manner which must give them a considerable resemblance to the drivers.^a

It is true, of course, that the keleps and the drivers are very distinct, but careful comparison will show that the differences are in degree rather than in kind. They represent possible developments from the same primitive system of organization, while to find a common starting point with the ants it may be necessary to go back to the nonsocial stage. Structurally, too, the keleps are very different from the drivers, but the genus *Cerapachys* and its allies are referred by some authors to the *Poneridæ* and by others to the *Dorylidæ*. It should be no more surprising that some of the habits of the true ants should be approximated by other groups of independent origin than that the bees and wasps, or that the true ants and the termites, should be so similar.

The idea that any existing group of organisms has given rise to another group is generally, and probably always, erroneous. With respect to any given character, one group may remain primitive while another has advanced, but nothing organic is stationary, and the fact that a plant or animal is primitive in one respect may well be taken as a suggestion that good progress has been made in some other.

Looked upon as ants, the kelep and its relatives are undoubtedly primitive, since they are more like wasps than like other ants, but the

^a "We were amazed at seeing ants an inch and a quarter in length and stout in proportion marching in single file through the thickets. These belong to the species called *Dinoponera grandis*. Its colonies consist of a small number of individuals, and are established about the roots of slender trees. It is a stinging species, but the sting is not so severe as in many of the smaller kinds."—Bates, H. W., 1875, *Naturalist on the River Amazon*, p. 9, ed. 4.

theory that their social organization must also represent the primitive condition of the true ants seems not to find confirmation in fact. The relatively small size of the colonies does not make them homologous with incipient ant colonies. They represent a different system of social organization. An increase in the size of the colonies of the keleps would not carry them in the direction of the true ants, but toward that of the drivers, unless they changed their habits and became vegetarians.^a

These various considerations do not exclude, of course, the possibility that some of the families now included among the true ants may have descended from Ponerid stock, but if so we may expect to find that their breeding habits are not those now ascribed to ants as a natural group, it being highly improbable that insects which had become completely socialized, like the keleps, should abandon this condition and return to the relatively crude and wasteful system followed by the ants and termites.

AMBIGUOUS USE OF THE TERM "SWARM."

Care has been taken in the preceding diagnoses of the types of social organization to refer to the simultaneous annual emergence of winged individuals of both sexes as a *concourse*, reserving the term *swarm* for its original use with the bees, and for an entirely analogous application to the kelep.

With the bee and the kelep the swarm is made up of workers (undeveloped females), and it is obviously incorrect, or at least very inexact, to apply the same word to a collection of winged adults of both sexes, as among the ants and termites.

Swarming, as with the bee and the kelep, is a process which does not take place at all in the other types of social organization. It results in the foundation of a new colony by the spontaneous subdivision of the workers of an older community, an occurrence not known among the termites and true ants.

The simultaneous emergence of the newly matured males and females from all the nests of the species has for its object cross-fertilization. It is a time specialization not attained by the honey-bees nor by the keleps, among which facilities for interbreeding are maintained throughout the season. The swarming of the bee and the kelep has, in fact, no connection with the cross-fertilization of the

^a If the laying of few eggs and living in small colonies is to be looked upon as a primitive character, the genus *Ponera* is the most backward of the American series of Poneridae and the kelep the most advanced. Such a criterion can not be applied at random, however, since specialization may tend toward restricted fecundity as well as in the opposite direction. Whether an insect would prosper best in colonies of 10, 100, or 1,000 would depend on its habits and environment.

sexual insects, which may take place either before or after the division of the colony.

DETERMINATE AND INDETERMINATE COLONIES.

An insect colony in which all the eggs are furnished by a single laying queen is a strictly determinate organization; that is, it reaches a natural limit after the mother insect dies or ceases to produce. The queens of ants and termites are sometimes enormously fertile and live for many years, so that determinate colonies may sometimes attain large size.

Colonies may be called indeterminate when the social economy of the insect is such that a lost queen can be replaced. This is the case with the honeybee, which may be said to have a simple indeterminate colony because each hive has but a single laying queen. Colonies with more than one egg-producing queen may be called compound indeterminate. This condition has been reached in two different ways. Some of the termites, for example, are able to replace a lost queen by what are called complemental queens, individuals which are brought to a precocious sexual maturity, but without becoming fully winged. Other termites, such as the South European *Termes lucifugus* studied by Grassi, seem to have gone over entirely to the complemental queen basis, thus reaching a completely indeterminate organization. With the ants the same result has been reached in a slightly different manner. Some of the young queens are fertilized and drop their wings before emerging from the parental nest, and, being tolerated by their mother and sisters, they remain to contribute to the numerical prosperity of the family.

A condition very similar, superficially, to that of the clustered colonies of the keleps is to be found in certain ants and termites which have the habit of making what might be called multiple nests. Instead of constructing a single compact dwelling, a colony may spread out into several distinct burrows or nests, connected by galleries, sometimes very long. An instance of this among the ants has been cited already on page 27. In one species of the termites, a single colony often builds numerous nests of considerable size on widely separated branches of the same or neighboring trees in the forests of Liberia. The queen, however, does not live in these aerial summer-houses, the eggs being carried up by the nurses through the galleries which connect with subterranean burrows.

It is conceivable, however, that the compound indeterminate colony might have originated in a more direct manner among insects which have never passed through the determinate stage of social organization. Social organization probably began, as already suggested, with

a condition of gregarious association of equal individuals. With the ancestors of the termites and ants this became gradually more centralized and specialized until a completely monarchical system was attained, which is still followed, at least in the early stages of new colonies.

With the kelep, however, there is no indication of a social history of this kind. The primitive society of equal individuals became specialized into two castes, the workers and the layers, so to speak, but there is nothing in the habits of the insect to indicate that there ever was a definite restriction to one fertile female for a colony.

COMPLETE SOCIALIZATION OF THE KELEP.

With the ants the colonies are founded by solitary queens and held apart by definite instincts of hostility, but the keleps separate into small colonies merely for economic reasons, as it were, to find new feeding grounds. The colony itself is a different social phenomenon in the two groups. Viewed from what might be called the geographical standpoint a colony in a new place is a new colony, however planted, but viewed from the standpoint of the insects and their social organization there is a fundamental distinction. A new colony of ants is really a new social group, a distinct family, but there are no such things, apparently, as new groups of keleps; there are only subdivisions of older groups. The female or queen ant leaves the old group and exists for a considerable period as a solitary independent insect, but there is no provision in nature for a solitary kelep. The kelep is completely socialized, if such an expression may be permitted, while the ant is not. Indeed, it may be claimed that the social organization of the kelep is more perfect than that of any insect whose life history has become known thus far. It is less specialized than that of the honeybee, perhaps, but is more complete, for even with the bees the young queens are obliged to leave the hive for the nuptial flight.

Complete socialization involves, apparently, the transfer of the chief responsibility, the social center of gravity, as it were, from the queens to the workers. The colonies of the bumblebees, wasps, and termites are governed, or at least founded, by the queen or mother; they represent the social principle of *matriarchy*, while colonies of the bees, keleps, and probably the drivers also, are founded and managed by the workers. In the matriarchy of the bumblebees, according to Maeterlinck, the queen-mother has to protect her eggs to prevent their being destroyed by her older daughters, but in the *ergatarchy* of the honeybees the queen is restrained by the workers from destroying her own fertile progeny and possible successors, against whom she entertains sentiments of deadly jealousy. It is not to be supposed, of course, that the queens of the ants and termites issue orders

or actively control the colony when once established, but even then there is an important difference in social economy, as pointed out in another place. The success or vital efficiency of a colony of ants or termites depends upon the number of sexual insects or royalties it can produce, but among the bees and keleps prosperity is measured, primarily, by the number of workers, which have become quite as necessary as the queens in the establishment of new communities.

The founding of a new colony among the ants and termites is an incident or direct sequel of the process of sexual reproduction. The sexual insects emerge simultaneously from the different nests of the species for their mating flight, but do not return, the few survivors remaining to found new colonies where chance has carried them. The workers do not figure in the *swarming* process at all; they function merely as nurses to assist the queen in raising their sexually mature brothers and sisters.

The honeybees have modified this programme to the extent that the young queen does not attempt, by herself, to establish a new community, but returns to her family after the mating flight.^a The keleps, however, have achieved a much more complete separation of their political system from strictly reproductive complications. The foundation of a new colony not only does not depend upon the initiative of the queen, but may be undertaken quite without her presence.

Cross-fertilization or interbreeding among the members of the species is undoubtedly a necessity for the keleps, as for all other highly developed organisms, but it may not be nearly as acute a requirement as among the termites, honeybees, and true ants, whose social systems make far greater demands for fecundity on the part of the queens. If, on the analogy of the bees, the eggs of an unfertilized queen will produce only males, the deficiency of the latter sex would be automatically made good for that particular neighborhood at least.

The predaceous habits, the winglessness of the workers, and the lack of any instinct to forage a long distance from the nest forbid the formation by the kelep of large communities like those of the bees, but this need not keep us from appreciating the advantages of the kelep organization, which by its greater mobility enables the insects to keep nearer the source of supplies without being obliged to waste so much energy as do the ants in carrying in their food, and without, like the drivers, giving up a settled existence altogether.

It becomes, also, even more obvious than before that the keleps may prove to have only the most superficial similarity to the ants, and that the social systems of the two groups may be of entirely independent development. The striking parallel between the bees and the

^a The impregnation of the young queen bee is said to take place occasionally during the swarming flight.

keleps does not prove, of course, a common descent from a social ancestor any more than does the agreement of the ants with the termites, or that of the bumblebees with the wasps. There are still many solitary bees among which a colony organization might grow up; also solitary wasps, some of which associate gregariously; and, finally, there are solitary wasps with wingless females which have undoubted relationships with the drivers and the keleps. The ant organization can hardly be looked upon as a further specialization from this series. The breeding habits prove conclusively that the history of the ants involves an independent specialization, probably from some nonsocial ancestry, but certainly not from one which had attained any such organization as the keleps or the drivers, or any such tendency to winglessness in the female sex as shown in the Mutillidæ and other related groups of parasitic wasps.

The feeding of the larvæ with captured insects by ants of the family Myrmicidæ has been cited by Professor Wheeler as evidence in support of a suggestion of Professor Emery that this family of ants was derived from the Poneridæ.^a But even if this correspondence be accepted as a true indication of relationship it can scarcely mean more than that the ancestors of the ants were predaceous insects like the keleps and the drivers. The latter groups have kept the predaceous food habits, but among the ants there is still to be found the even more primitive instincts of an annual emergence of both sexes from the nest and the founding of new colonies by solitary females.

On the other hand, it must be admitted that the habits of the genus *Stigmatomma*, as described by Professor Wheeler, offer many more points of resemblance to those of the kelep than do those of *Ponera* and the Texan genera *Pachycondyla* and *Leptogenys* studied by Professor Wheeler. The larva of *Stigmatomma*, which "does not conform to the Ponerine type," is much more similar to that of the kelep, as are also the eggs.

^a"There still exists an ecological (or biological, in the German sense) connection between the Ponerinæ and the Myrmicinæ, as I have lately ascertained. Since describing the peculiar method employed by the Texas Ponerinæ in feeding their larvæ, I have found, that one of our New England Myrmicine ants, *Stenamma* (*Apharnogaster*) *fulvum* Rog., subsp. *aquila* Buckl., var. *piccum* Emery—an ant very common under stones and in rotten logs along the edges of woods—has essentially the same method of feeding its young. My attention was first called to the fact in an artificial nest belonging to Miss Adele M. Fielde, at Woods Holl, Mass. One afternoon Miss Fielde left a lot of queen pupæ and larvæ of *Crematogaster lincolata* within reach of the *Stenamma* colony. By the following morning the *Stenammæ* had carried these into their nest, cut off their heads and abdomens, and had distributed the pieces freely among the larvæ, which could be seen singly and in groups of from two to five eagerly feeding on the juices in the same manner as Ponerine larvæ."—Wheeler, W. M., 1901, Biological Bulletin, 2: 65.

It becomes apparent that the species of so-called Poneridæ or Ponerinæ of which the habits are known belong to five different natural groups which are likely to be recognized at some future time as distinct families; at least the differences of habit and social organization are as great or greater than those of many families or orders among the higher plants and animals. It is becoming more and more appreciated that such characteristics afford as good or better indications of evolutionary history than do mere differences of structure and proportions. Indeed, the evolutionary significance of a structural character can not be determined until the biology of the plant or animal is known—that is, its mode of existence and place in the economy of nature.

There may be said to be two methods of classification, corresponding to the two states of knowledge regarding a group of animals or plants. Under what may be called the analytical system, classification is based primarily on a logical analysis of formal characters, the various groups, such as orders, families, genera, and species being reached from the top downward by repeated subdivision. The concrete or synthetic method reverses this procedure. Coherent groups of normally interbreeding individuals are recognized as constituting species; closely allied species are grouped into genera, and genera into families.

Owing to their vast numbers and diversity, the classification of insects is still largely in the analytical stage, so that recognition of the kelep as representing a distinct family would not be consistent with the current classification. Nevertheless, it may be fully expected that in due time the insect groups will be treated in better accord with the methods by which the mammals, birds, and other higher animals are classified.

The five groups referred to above may be typified by the genera *Stigmatomma*, *Odontomachus*, *Ponera*, *Pachycondyla*, and *Ectatomma*. The first and second groups have already been recognized as families or subfamilies because of structural peculiarities of the adult insects, the Amblyponinæ (including *Stigmatomma*) having no deep constriction behind the node or first abdominal segment. The Odontomachidæ are characterized by their remarkable mandibles, which are inserted close together near the middle of the head instead of at the anterior corners, as in all the related groups. The true Poneridæ, as represented by the typical genus *Ponera*, show the most backward stage of social organization and have very small colonies. The larvæ are provided, according to Professor Wheeler, with four pairs of peculiar adhesive dorsal tubercles, supposed to have the function of holding them in position against the sides of the nest chamber. In *Pachycondyla* and *Leptogenys* the larvæ are, like

SYNOPSIS OF TRIBES OF PONERINÆ.

1. Claws simple ----- 2
Claws pectinate----- 5
2. Hind tibiæ with *one* apical spur----- 3
Hind tibiæ *without* an apical spur-----Tribe I. ONYCHOMYRMICINI
3. Promesonotal suture usually present; apex of the abdomen from the third segments normal, not curved downward, but porrect----- 4
Promesonotal suture wanting or obsolete; apex of the abdomen from the third segment abnormal, curved downward in such a way that it is directed forward beneath; antenna ending in a distinct club.
Tribe II. CERAPACHYINI
4. Head oblong, the eyes *not* especially small, placed at or a little *beyond* the lateral middle; thorax not constricted at the middle.
Tribe III. PROCERATIINI
- Head oblong or oval, the eyes usually small, oval, placed *before* the lateral middle sometimes near the base of the mandibles (in a single case very minute and placed at the middle)-----Tribe IV. PONERINI
5. Head oblong oval, the eyes not small, placed near the lateral middle, thorax long, slightly constricted before the middle, the metanotum longer than the mesonotum, convex above; mandibles subtriangular, curved downward with an oblique but broad masticatory edge.
Tribe V. LEPTOGENYINI, ^a

SYNOPSIS OF TRIBES OF PACHYCONDYLINÆ.

1. Claws cleft or *with* a tooth beneath----- 6
Claws simple *without* a tooth beneath----- 2
2. Head usually oblong, the eyes, when present, never large; thorax usually with one or more sutures; if without sutures, the head, thorax, and first two segments of the abdomen are longitudinally grooved----- 3
Head quadrate or subquadrate, very little longer than broad, the eyes very large, placed at the sides close to the base of the mandibles; the thorax oblong, subquadrangular, without sutures above or with only the metanotal suture present; scale of abdominal petiole subquadrate.
Tribe I. LIOPONERINI
3. Head variable, although usually oblong, but *not* longitudinally grooved, the eyes rather small oval or oblong oval, placed anteriorly *before* the lateral middle, sometimes near the base of the mandibles; mandibles usually more or less triangular, the masticatory margin dentate; if slender, the

^aTribe I. Onychomyrmicini: Represented by a single genus, *Onychomyrme* Emery, found in India.

Tribe II. Cerapachyini: Well represented in America. The genera are: *Sphinctomyrme* Mayr, *Phyracaces* Emery, *Cerapachys* Smith, *Parasyrcia* Emery, *Syscia* Roger, and *Cystias* Emery.

Tribe III. Proceratiini: Genera: *Discothyrea* Roger, *Sysphincta* Roger, *Proceratium* Roger, and *Prionopelta* Mayr.

Tribe IV. Ponerini: A group of world-wide distribution. Genera: *Centromyrme* Mayr, *Trapeziopelta* Mayr, *Myopias* Roger, *Cryptopone* Emery, *Rhopalopone* Emery, and *Ponera* Latreille.

Tribe V. Leptogenyini: A tribe readily recognized by its members always having the claws pectinate. Genera: *Prionogenys* Emery, *Leptogenys* Roger, *Lobopelta* Mayr, and *Simopone* Forel.

mandibles have a large tooth within near the middle: thorax narrowed posteriorly, with all the sutures, or at least the promesonotal suture, present; first abdominal segment well separated from the second by a strong constriction and a movable joint ----- 5

Head oblong, sometimes longitudinally grooved, the eyes, when present, oval or oblong, placed on the sides near or a little *beyond* the middle, never far anteriorly; mandibles most frequently rather long and narrow, with teeth along the inner margin; if triangular, the masticatory margin is edentate; thorax rarely much narrowed posteriorly, the sutures sometimes present, sometimes wholly absent; first abdominal segment *not* well separated from the second, usually broadly sessile with it, and without a movable joint between ----- 4

4. Head, thorax, and first two segments of the abdomen *not* longitudinally grooved, the sutures of the thorax distinct; mandibles rather long and narrow, acute at apex, and armed with teeth along the inner margin; eyes sometimes absent; if present, oval, placed at or near the middle of the sides of the head ----- Tribe II. AMBLYOPONINI

Head, thorax, and first two segments of abdomen longitudinally grooved, the sutures of the thorax entirely absent; mandibles obliquely truncate at apex, *without* teeth; eyes oblong, placed on the sides of the head a little behind the middle; scape of antenna short, not half the length of the head ----- Tribe III. CYLINDROMYRMICINI

5. Thorax always narrowed posteriorly, with the pro-, meso-, and metanotal sutures usually present, or at least with the pro- and mesonotal sutures present, scape of antenna long, usually reaching to the apex of the head or nearly to it; scale of abdominal petiole usually higher than long; eyes placed on the sides of the head, usually between the middle and the base of the mandibles, rather close to the mandibles.

Tribe IV. PACHYCONDYLINI

6. Thorax rather long, narrowed posteriorly much as in the *Pachycondylini* and with usually one or more of the notal sutures present, the sides never parallel, usually more or less constricted medially, but never strongly constricted, mandibles never very long, and *not* curved upward, usually with a slight curve downward; head oval-quadrate or oblong, the eyes not large, placed on the sides, usually a little *before* the middle, rarely behind the middle ----- Tribe V. ECTATOMMINI

Thorax very long and cylindrical, the sides parallel, or nearly, the pronotal suture alone distinct, the meso- and metanotum closely united *without* a trace of a dividing suture; mandibles abnormal, very long, slender, and curved upward, the inner margin from the basal angle armed with two rows of minute teeth; head oblong, the eyes large and placed close to the base of the mandibles ----- Tribe VI. DREPANOGRAPHINI.^a

^a Tribe I. Lioponerini: Represented by a single genus, *Lioponera* Mayr.

Tribe II. Amblyoponini. Genera: *Myopone* Roger, *Mystrium* Roger, *Emergella* Forel, *Stigmatomma* Roger, *Mesoxena* Smith, and *Amblyopone* Erichson.

Tribe III. Cylindromyrmicini: A tribe found only in the Americas and represented at present by two genera, *Cylindromyrmex* Mayr, and *Thaumatomyrmex* Mayr.

Tribe IV. Pachycondylini: This tribe is well represented in America, Asia, and Africa, probably a dozen genera being already characterized. Those known to me are: *Odontoponera* Mayr, *Diacamma* Mayr, *Plectroctena* Smith, *Bothrioponera* Mayr, *Belonopelta* Mayr, *Pseudoponera* Emery, *Brachyponera* Emery.

It is worthy of notice that Doctor Ashmead finds structural characters which require the separation of *Leptogenys* from *Pachycondyla*, *Neoponera*, and other immediately related genera. The fact that Professor Wheeler found the habits, eggs, and larval characters of *Leptogenys* and *Odontomachus* so closely similar to those of *Pachycondyla* only increases the significance which may well be attached to the differences in these respects between *Ectatomma* and the *Pachycondyla* series.

HABITS OF PONERIDÆ.

The habits of the insects of the family Poneridæ, with which the kelep would be associated in current zoological classification, were almost completely unknown until the recent investigations by Professor Wheeler. It is evident, however, from his interesting papers, that the Texas Poneridæ studied by him must belong to series quite remote from the kelep. The eggs of the kelep, for example, are elliptical in shape and not cylindrical, as in *Odontomachus* and in the Poneridæ investigated by Professor Wheeler.

The breeding habits and the characteristics of the eggs and larvæ of the Ponerinæ exhibit striking deviations from those of other ants. I have not seen the eggs of *Odontomachus*, but throughout the month of May I have often happened on the eggs of *Pachycondyla* and *Leptogenys*. These are white and of a slender, oblong shape, somewhat smaller in the latter than in the former genus. They differ in shape from the eggs in species of *Eciton*, *Camponotus*, *Formica*, *Pogonomyrmex*, *Solenopsis*, and *Tapinoma*; for the ants of these genera, representing several subfamilies, agree in having elliptical and much less slender eggs than the Ponerinæ. The Ponerinæ also keep their eggs in more regular packets, the long axes of the different eggs being placed parallel with one another.^a

It would probably be an advantage for the kelep to have eggs like those of the *Odontomachus*, which readily adhere in bundles and can be the more easily carried, but the difficulty is overcome by the greater intelligence of the kelep, which adroitly uses the posterior end of its

Mesoponera Emery, *Pachycondyla* Smith, *Euponera* Ford, *Neoponera* Emery, and *Ectomomyrmex* Mayr. The genera *Psilidomyrmex* André, and *Heteroponera* Mayr, which I have not seen, appear to belong to this tribe.

Tribe V. Ectatommini: This tribe is abundantly represented in Central and South America and in Africa. Only a few forms occur in North America, and these in the Southern States. The genera placed here at present are: *Platythyrea* Mayr, *Alfaria* Emery, *Ectoponera* Mayr, *Ectatomma* Smith, *Gnampetogenys* Rogers, *Acanthoponera* Mayr, *Paraponera* Smith, *Holcoponera* Mayr, *Rhyttoponera* Mayr, *Streblognathus* Mayr, *Dinoponera* Roger, *Paltothyreus* Mayr, and *Magaponera* Mayr.

Tribe VI. Drepanognathini: This is a peculiar little group known only from Asia and Africa, and but few species have been described, all falling into a single genus, *Drepanognathus* Smith.

^a Wheeler, W. M., 1901, Biological Bulletin, 2:14.

abdomen to load several eggs between its mandibles. Sometimes also the eggs of the kelep adhere somewhat in irregular clusters, so that several can be lifted and carried at once.

The superior social organization of the kelep is also rendered evident by important differences in feeding habits.

The Ponerine do not seem to feed one another, like the specialized ants. In captivity *P. harpar* would eat the yolk of an egg or even sugar, but it would not eat termites. *L. elongata* devoured termites and small caterpillars with avidity, but would not eat flies. *O. harmatodes* is more omnivorous; besides caterpillars, house flies, beetles, and small Hemiptera, it will eat sugar, bread, cake, etc.^a

The kelep does not appear to have the art of regurgitating food as do the true ants, but it is the regular custom of the workers to gather up on their mouth parts large drops of nectar, sirup, or honey, which are carried into the nest and freely dispensed to the remaining members of the community, as well as to the queen and larvæ. The use of nectar and other sweet substances by other Poneridæ seems not to have been reported. The adult keleps seem to be able to live for an indefinite period on sugar alone, though animal food is probably necessary for the normal growth of the larvæ. Termites and insects of all the principal groups are eaten readily.

The extent to which the keleps normally depend upon nectar has not been adequately learned as yet. It may be that they use it largely, if not exclusively, for feeding the very young larvæ, since these do not seem to be regularly fed with animal food, captured insects always being given, as far as observed, to the large larvæ. Colonies fed exclusively on sugar or honey have raised larvæ to nearly the full size, but these seldom, if ever, pupate normally; and in some of the captive colonies very few pupæ have survived to emerge as adults. Sometimes the cocoons are opened and the pupæ taken out and eaten; in other instances they are thrown on the bone yard or refuse heap which each colony maintains. Messrs. Lewton and McLachlan are inclined to believe, after a series of very careful observations, that this mortality is sometimes due to the attacks of the mites, especially when colonies become weak and discouraged. Prosperous colonies, on the other hand, may receive no aparent injury from the presence of large numbers of mites.

The most prosperous of the colonies which have been kept under laboratory observation is one at Victoria, Tex., which was used as the basis of a feeding experiment to see how many boll weevils it would destroy. From 10 to 30 weevils a day was the regular ration,

^a Wheeler, W. M., 1901, Biological Bulletin, 2:11. Mr. McLachlan reports that a colony of *Pachycondyla harpar*, captured near Victoria, devoured termites greedily.

but in one instance over 50 weevils were killed inside of twenty-four hours, and in the course of the experiment the colony disposed of between 1,200 and 1,500 weevils.

The nests of the keleps, though small and simple, in comparison with those of the termites and true ants, consist of chambers several square inches in extent, with level floors and arched roofs, and denote a state of architectural advancement much greater than that reported by Professor Wheeler in the Texan genera studied by him.

The nests of the three Ponerinæ agree in being of a very primitive structure. They consist of a few simple and irregular burrows, or galleries, some of which run along the surface of the soil immediately beneath the stone or log, while others extend down into the soil obliquely or vertically to a depth of 8 or 10 inches. These burrows may anastomose, but they are not widened at certain points to form chambers, as in the nests of the more specialized ants (*Atta*, *Pogonomyrmex*, *Camponotus*, etc.). Even in artificial nests of the Lubbock pattern the Ponerinæ dig only anastomosing galleries scarcely more than a centimeter in diameter.^a

TEMPORARY BROOD CELLS OF THE KELEP.

The alliance of the kelep system of organization with that of the wasps and bees receives support also from the instinct of inclosing the pupating larvæ in what may be termed temporary brood cells. It has been reported of some ants and of some genera of Poneridæ that they bury their larvæ before pupation. The kelep, instead, constructs over them a cell of earth, if no other materials are at hand, but prefers pieces of old cocoons if these are obtainable.^b

The bees and wasps avoid the labor of inclosing each wriggling larva separately by a system of permanent brood cells in which the larvæ are reared, and which have merely to be sealed over at pupation. Many of the true ants (and also the drivers) have abandoned the use of cocoons and of the brood cells in which they can be spun. With them the digging of extensive subterranean nests and the careful handling of the larvæ have made external protection unnecessary. Nevertheless, the failure to make brood cells deprived the

^a Wheeler, W. M., 1901, Biological Bulletin, 2: 3.

^b The honeybee also makes use of silk from old cocoons in the construction of brood cells.

"Into the material used in constructing brood combs bees often incorporate bits of wax and fiber-like gnawings of cocoons from old combs in which brood has been reared, and if given cappings or trimmings of combs they will work them all over and utilize most of the material. Also when the bees have abundant supplies of pollen much of this is incorporated into the material of brood combs, thus saving the costlier substance—wax."—Benton, Frank, 1899, The Honey Bee, Bul. 1, n. s., Division of Entomology, U. S. Department of Agriculture, p. 27.

ants of the possible evolution of the art of storing liquid food like the bees.^a

The position of the brood cells has doubtless had an important influence on the evolution possible to the different groups of social insects. The brood cells of the kelep are built over the larva as it lies on the floor of the chamber. Those of the honeybee are also horizontal, though piled, as it were, in double tiers. The cup-like cells of the bumblebees stand erect.

The instinct of making honeycomb was evidently attained as a further step in the practice of constructing permanent brood cells in advance of the egg laying. Among insects, as with man himself, progress toward civilization has largely come through the accentuation of parental instincts.

The underground activities of the keleps are much less extensive than those of the ants. The galleries of their nests are simple and nearly straight, and the chambers relatively small. There are none of the winding passages to which the termites and true ants are so partial, and which make the complete investigation of their domestic habits so difficult.

WEEVIL-STINGING WASPS.

The incredulity with which the report of the weevil-stinging ant was received by entomologists shows how completely incongruous such a habit appeared when ascribed to an ant. The biological anomaly largely disappears, however, with the recognition of the fact that the natural relationships of the kelep lie with the parasitic wasps rather than with the ants. The stinging of other insects by predaceous wasps is an old and familiar fact. It is true that most wasps prey upon spiders, caterpillars, flies, cicadas, crickets, cockroaches, or even upon bees or ants; but there is one family, the Philanthidae, which regularly attacks beetles. One of these wasps even makes a specialty of beetles of the weevil family.

The species of the genus *Cerceris* are numerous in Europe, and several of them are known to make burrows in the ground and store them with beetles for the benefit of the future larvæ. The beetles chosen differ in family according to the species of *Cerceris*; but it appears from the observations of Fabre and Dufour that one kind of *Cerceris* never in its selection goes out of the limits of a particular family of beetles, but, curiously enough, will take insects most dissimilar in form and color provided they belong to the proper family. This choice, so wide in one direction and so limited in another, seems to point to the existence of some sense, of the nature of which we are unaware, that determines the selection made by the insect. In the case of our British species

^a "Though also making special 'honey tubs,' some of the bumblebees commonly use old brood cells for the storage of honey."—Sharp, David, 1901, Cambridge Nat. Hist., Insects, 2: 56.

of *Cerceris*, Smith observed *C. arenaria* carrying to its nest Curculionidæ of very diverse forms, while *C. labiata* used a beetle—*Haltica tabida*—of the family Chrysomelidæ.

The beetles, after being caught, are stung in the chief articulation of the body, that, namely, between the pro- and meso-thorax. *Cerceris bupresticida* confines itself exclusively to beetles of the family Buprestidæ. It was by observations on this insect that Dufour first discovered the fact that the insects stored up do not decay; he thought, however, that this was due to the liquid injected by the wasp exercising some antiseptic power; but the observations of Fabre have shown that the preservation in a fresh state is due to life not being extinguished; the stillness, almost as if of death, being due to the destruction of the functional activity of the nerve centers that govern the movements of the limbs.^a

Between the habits of such wasps and those of the keleps the differences are certainly less than between the keleps and the true ants, and another wasp of the same family shows how the transition from the parasitic to the predaceous stage could be passed very gradually. Instead of concluding its maternal duties by stocking its nest or burrow with paralyzed insects in advance, *Philanthus apicorus*, which preys upon the domestic honeybee, provides only one individual at first and returns later to bring others, as required by the growing larvæ. Moreover, it has the habit of crushing its prey in its mandibles, thus giving the larva easier access.^b The kelep system represents a further improvement, the captured weevils being pulled to pieces and distributed to numerous larvæ. In one group of Hymenoptera, the sawflies, the larvæ have well-developed legs and are able to crawl about like caterpillars, which they very much resemble. In all the other families the larvæ are legless, helpless grubs. Most of them are, in the larval stage, parasites, either of plants or of animals. Those which are not parasitic require, obviously, to be fed and cared for by their mothers, a condition most conducive, obviously, to the development of social habits.

The distinction between predaceous and parasitic habits is not easy to draw. Mrs. Cook saw three young kelep larvæ at one time attached to a termite which the workers were still carrying about to feed to the larger larvæ, which seem to secure nearly all of the direct attention of the workers. If the prey remained alive such attached larvæ would be looked upon as parasites.

The manner in which the keleps feed their prey to their larvæ is thus to be looked upon as a derived rather than as a primitive trait, compared with the habits of the other carnivorous Hymenoptera.

^a Sharp, David, 1901, Cambridge Nat. Hist., Insects, 2:125.

^b There are two other significant approximations of habits between the kelep and these wasps of the family Philanthidæ. They seize their prey in their mandibles and sting it by bending the body around underneath, to reach the vulnerable point. *Philanthus* also makes long burrows in the ground, with chambers at the end in which the eggs are laid and the young reared.

The parasitic groups avoid all further labor in behalf of their young by simply laying their eggs inside the victim, upon which the larvæ feed at pleasure. The solitary wasps stock their brood cells in advance with whole spiders or insects. Some of the social species comminute or mangle their prey, and others, including many of the true ants, regurgitate the partly digested food material. The drivers probably feed dismembered pieces of their prey like the keleps. The kelep larvæ are not so completely helpless as those of bees and true ants, being provided with mouth parts adapted for eating out the soft interior tissues of insects, and long, flexible necks to enable them to reach inside and clean out the sections of boll weevils laid by the workers carefully on the fat stomachs of their baby sisters. Two such, lying side by side, each provided with a weevil's front leg to nibble, was the ludicrous sight observed in the nest of one of the captive colonies in Texas. Mrs. Cook has noted another instance of feeding which well illustrates the extent to which the social organization has developed in this respect.

A worker seized a termite as soon as it was dropped into the nest and held it in its jaws for fully five minutes, the termite vigorously protesting with its antennæ. After it was dead, or at least motionless, the kelep took it below where other workers assisted in feeding it to a large larva. It was very hard to get the termite properly placed; time and again it fell from where it had been put, and was turned over and twisted in all sorts of ways in the effort to bring it into a position so that the larva might take hold of its head. The larva meanwhile moved its own head back and forth, evidently trying to get hold on its own account, and a little larva near by did secure a hold on the other end of the termite, so that the keleps had to move both larva and termite in their further efforts to give the latter to the large larva. The little larva was almost as large as the termite. Finally the matter was arranged, the termite lying across the two larvæ, which remained peacefully side by side, the big one eating at the head, the little one at the tail. A worker had to take the head of the big larva between his jaws and fore legs and put it in contact with the termite, and then stood over it as though to see that the larva did its duty. The weight of the small larva kept pulling the termite off the body of the large larva before it had become firmly attached, so a worker stayed by and kept pulling the termite back in position. Finally the large larva got to work in earnest, and the faithful nurse left to help another kelep with another termite.

USE OF FIBERS IN CONSTRUCTION.

A possible reminiscence of an upper air existence by social ancestors of the kelep is to be found in a curious tube or gallery which is often constructed at the entrance of the nest to extend the underground passage upward on the stem of the cotton plant or other object to which the opening of the nest is adjacent. The workers always prefer to dig against something rather than in the open ground. The tubular structure in question may be only an inch or less in length, but it sometimes extends upward for 5 or 6

inches. It is built of shreds of woody material, bark, fibers, or even of cotton lint, sometimes with pellets of earth intermingled, but usually thin and with something of the papery texture and appearance of a wasp's nest. The object of this curious structure has not been determined with certainty. In some situations it serves the purpose of keeping the loose earth from falling into the burrow and may afford protection against enemies of some kind as yet unknown. After the tube has been built the insects seem reluctant to crawl over it to the ground outside. They even carry the pellets of earth brought out of the burrow up the stem of the plant and far out on the branches, and then drop them off.

STINGING HABITS OF THE KELEP.

The most obviously wasp-like habit of the kelep is, of course, the adroit stinging of its prey to produce paralysis and consequent helplessness. It has long been known that the mud daubers and the digger wasps stock their brood cells in advance with paralyzed insects or spiders, though very few of them are known to attack beetles. The insects are permanently paralyzed, but not killed outright, and afford the young wasps an adequate supply of fresh food on which to grow to maturity before emerging from the cell in which the egg was deposited by the mother insect. It has been claimed by some observers that paralysis results because the insects captured by the wasps are always stung in a nerve ganglion. This extreme refinement of instinct is doubted by some, but seems to have been established by careful observers.

In dealing with the boll weevil there can be no doubt that the kelep shows great instinctive skill, and often persistence as well, for the armor of the weevil permits the insertion of the sting at only two points—on the middle line of the ventral surface, at the two joints of the body, one between head and thorax, the other between the two parts of the thorax. The difference in the use of the sting between the keleps and the true ants is most effectively shown when representatives of the two groups are brought together and permitted to fight. The ant tries to bite its antagonist, the kelep to sting and paralyze, the latter strategy being much more effective.

This habit of stinging other insects allies the kelep not only with the predaceous wasps, but also with the Mutillidæ and other parasitic groups, which, instead of preying on other insects or storing them up for their young, lay their eggs in the living insect direct or in the nests of the social Hymenoptera. The stings of the worker bees and ants are, as is well known, merely modified ovipositors. The males do not have stings, and the tendency to use them is generally less in the queens, in which the egg-laying function remains predominant.

Contrasts between the kelep and the true ants also appear in connection with the sting. The kelep, which has an effective sting for use on other insects, does not make it a weapon for general defense against intrusion. The ants, on the other hand, fight each other with their mandibles, but many of them sting viciously at any foreign object with which they may come in contact. Curiously enough, too, many ants in which the sting has become a mere harmless rudiment still go through the motions of stinging with as much promptness and apparent gusto as their more effectively armed relatives. The decline of the sting among some of the ants may be associated perhaps with the fact that they are vegetable feeders. At least, it would seem to be an indication of their remoteness from the parasitic groups of Hymenoptera.

HARMLESSNESS OF THE KELEP TO MAN.

Lest the present recognition of the similarity of the kelep to the bees and wasps should lead to another misapprehension, it may be well to repeat here the fact that the insect is entirely harmless to man. Its sting is used with instinctive promptness to paralyze boll weevils and other insects which it undertakes to capture, but there seems to be a complete lack of any tendency to defend itself by stinging, except when actually caught and held.

This has been shown to the entire satisfaction of all who have had the interest to watch the kelep colonies which were brought to the United States in July (1904). The insects have been handled on many occasions, and by many different persons, without any threat or symptom of stinging, except in the case of two or three young men at Victoria, Tex., who had the curiosity to make a test of the injury which the insect's venom could inflict. The result was quite the same as we had experienced in Guatemala, a slight and temporary irritation. Messrs. Goll and Collins, who recently excavated the nests of about 40 colonies in Guatemala, were not stung at all, though taking no measures to protect themselves.

That an insect which is so ready and skillful in stinging its prey should be so peaceable and harmless in other respects may well appear almost incredible, but a similar specialization of instinct is known to exist in the domestic honeybee, where the queen has no inclination to use her sting except for the purpose of dispatching her rivals.^a

^a "But though this sting is always ready to strike, though they make constant use of it in their fights among themselves, they will never draw it against a queen; nor will a queen ever draw hers on a man, an animal, or an ordinary bee. She will never unsheath her royal weapon—curved, in scimitar fashion, instead of being straight, like that of the ordinary bee—save only in the case of her doing battle with an equal—in other words, with a sister queen."—Maeterlinck, M., 1901, *The Life of the Bee*, 100.

ADAPTABILITY OF KELEP ORGANIZATION TO AGRICULTURAL PURPOSES.

It is plain that the size attained by the colonies and the fecundity of the individual queens by no means determine the rate of increase possible for such an insect as the kelep. A social economy which provides for an indefinite increase of the numbers of colonies and of laying queens may more than compensate for the absence of the exceptional productiveness of the queens of the termites and the true ants. The marvelous fecundity of the females in these groups is, indeed, to be looked upon as an adaptive specialization by which the species is able to maintain an existence in spite of adherence to a most wasteful social policy, in which so much is staked on the vicissitudes of a simultaneous annual emergence of all the young and unprotected individuals of both sexes. This precarious period in the life history of the ants has been well described by Professor Wheeler.

The sexual individuals, when finally liberated from the nests, are thrown on their own resources, and for a time the struggle for existence sets in with great severity. One has an opportunity of actually witnessing both catastrophic and personal elimination, often on a magnificent scale. The struggle among the males for the possession of the females is intense. The lives even of the fortunate among the former are rapidly extinguished. The surviving fecundated queens set to work to establish their colonies, an arduous and complicated undertaking, which ruthlessly eliminates all the poorly equipped. Even before they can dig their nests hundreds of these insects are devoured by birds, lizards, spiders, etc. And many more of them die from exhaustion while digging their nests, or from hunger while raising their first litter of young, or from the attacks of subterranean predatory insects, parasitic fungi, etc. This struggle, however, terminates on the appearance of the first workers, and the successful queens thenceforth again lapse into a condition of domestication till the close of their often very long lives.^a

The contrast can best be expressed, perhaps, by saying that the social system followed by the termites and true ants involves the loss of nearly all of the females, while in that of the keleps all females are, or may be, saved and utilized in the increase of the species. There is nothing to show that the very large colonies of the ants and termites are an arrangement advantageous to the species as a whole. They are rather the result of the failure of these insects to adopt the habit of swarming, as practiced by the honeybee and the kelep.

From the agricultural standpoint, too, the superiority of the kelep organization is obvious. The division of the species into small bands enables the insects to spread uniformly over the fields, while large isolated ant-hills inhabited by hostile colonies would exclude the possibility of an efficient protection of all the cotton. The hills and pit-

^a Wheeler, W. M., 1902, *Science*, n. s., 15: 769.

falls made by many ants would be a serious inconvenience in the cultivation of the crop. To avoid them would be difficult, and to drive over or plow through them would mean the wholesale destruction of the insects, so that the utilization in agriculture of a true ant-hill ant might well be deemed improbable. The social organization of the kelep avoids all of these difficulties. The colonies are small, but not hostile, so that all the plants of the field can be visited. Instead of an ant-hill and a maze of underground passages, they have a simple burrow, deep enough to give them protection against injuries incidental to ordinary cultivation. If the entrance is accidentally closed the inhabitants can readily reopen it; and if the situation proves to be inconvenient the whole community generally has the intelligence to move over close to the cotton plants, on which it regularly forages for nectar and game.

SUMMARY.

In summarizing the former report, of July, 1904, the investigation of the kelep was divided into five phases or questions, upon three of which evidence was submitted, while two others remained unconsidered. The three facts which seemed to be established were:

(1) The kelep protects the cotton plant against the boll weevil, which it regularly kills and eats. In the presence of sufficient numbers of keleps the protection is entirely adequate, as shown by comparative field tests in Guatemala. The keleps have made it possible for the Indians to maintain a field culture of cotton in the presence of the weevil, and have thus enabled the Indian variety of cotton to develop weevil-resisting characters which give partial protection, even in places where the keleps are few or wanting.

(2) The kelep does not attack plants, or have any other habits which would make its introduction into the United States injurious or undesirable.

(3) It is feasible to bring colonies of the insects to Texas and establish them in the cotton fields.

The continued study of the insect has furnished, of course, many additional data bearing upon the above statements, but all have been of a confirmatory nature. The present paper deals with the further question, whether the habits of the insect will enable it to breed and multiply in captivity or as a domesticated inhabitant of the cotton fields of our Southern States. From the analogy of the habits of the ants, it appeared to specialists in the study of that group of insects that the kelep could not be applied to agricultural uses. The facts detailed in the present paper seem to warrant a different answer.

(4) The kelep is not a true ant, but has a distinct type of social organization, much more like that of the domestic honeybee.

The utility of the kelep will depend, therefore, upon the answer of the remaining question, whether the kelep can survive and multiply under conditions of climate, soil, and food supply to be found in the United States. In structure, habits, and instincts it is wonderfully adapted to the work of destroying the cotton boll weevil.

It is, in short, a new and efficient insectivorous animal, in all probability capable of being utilized for the protection of cotton and other crops in many tropical and subtropical regions, whatever may be the results of the present effort to naturalize it in Texas.

It is still impossible to predict the fate, in a new country, of an insect which has so recently become an object of scientific study, but whatever the experiments may ultimately show regarding its ability to become established and thrive in the United States, it seems certain that the social organization of the species does not disqualify it for a future of agricultural utility. To prejudge its prospects by reference to the habits of the true ants would be the same kind of error as to discredit the honeybee on the ground that the bumblebees and wasps are worthless and undesirable insects.

Recent advices from Texas, received just as this paper is being completed, seem to indicate that the colonies which have been left out in the open ground of the cotton fields, without care or food, will not survive the winter, though they have lived long enough to show that low temperature alone is not fatal, thus confirming the result of a cold-storage experiment made in Washington last August (1904). As already explained in the present paper, the colonies of the first importation were far too small to make the experiment a fair one, and they were planted in Texas after the middle of July (1904), much too late in the season. A knowledge of the social organization of the insect will permit these and other obstacles to be avoided in the importations to be made in the coming spring (1905), and it is hoped that a satisfactory and conclusive test will result.

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